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Genetic Variation and Seed Transfer Guidelines for Ponderosa Pine in Central Oregon

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Abstract

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Adaptive genetic variation in seed and seedling traits for ponderosa pine from the east slopes of the Cascade Range in Oregon was analyzed by using 307 families from 227 locations. Factor scores from three principal components based on seed and seedling traits were related by multiple regression to latitude, distance from the Cascade crest, elevation, slope, and aspect of the seed source and by classification analysis to seed zone and 300-meter elevation band within zone. A provisional transfer risk equation and tentative new seed zones were delineated to guide seed transfer in artificial regeneration.

Keywords: *Pinus ponderosa*, seedlings, provenance, geographic genetic variation, ecological genetics, genecology, genetic diversity.

Summary

Wind-pollinated cones were collected from 307 trees at 227 locations uniformly distributed along the east slopes of the Cascade Range of Oregon and southeast into the Warner Mountains; a lighter sampling was done in the Ochoco Mountains and at several isolated locations in the high desert steppe. Four principal components were derived from seed size, germination, and seedling growth traits in four common-garden environments. Factor scores for the principal components were related to source latitude, distance from the Cascade crest, elevation, slope, and aspect by using a multiple regression model, and to seed zones and 300-meter elevation bands in zones by using a classification model.

Elevation dominated the geographic variation pattern, but interactions between location variables, including slope and aspect, also were significant for most principal components. The component of variance for location exceeded the component of variance for families in locations only for factor scores of principal component-1, which was associated with seedling vigor. Lack of fit to the models was about the same for regression and classification analyses and was very highly significant for all principal components.

Seedlings from low elevation, even if desert-fringe, low-site sources, were the most vigorous in the common garden. The overall importance of elevation and the local situation associated with three areas that deviated from the general elevational pattern indicated that for seedling vigor, genetic differentiation across temperature gradients was much stronger than across moisture gradients.

For purposes of seed transfer, a provisional risk equation based on the first three principal components is provided, and tentative new seed zones are delineated.

Introduction

Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) has a very extensive range in Western North America. Populations in central Oregon belong to the North Plateau race of the species, as outlined by Conkle and Critchfield (1988), and represent the most southwesterly populations of that race. The Cascade Range physically separates the North Plateau and Pacific races, except in southern Oregon north of the Klamath River where they are contiguous.

Although geographic variation in ponderosa pine has been studied extensively (references in Conkle and Critchfield 1988), the Oregon part of the distribution has been represented weakly or not at all in these tests. The present study looks at this area in detail and includes seed sources from the Columbia River (ca. 45°30' N. lat.) south along the east slopes of the Cascade Range to the Oregon-California border (42° N.) and east through the Warner Mountains in southern Oregon. The purpose of the present work, from common garden studies, is:

1. To describe the genetic-geographic patterns in variation in seed and seedling traits.
2. To relate patterns of variation (a) to the geographic and topographic features of the landscape and (b) to zones depicted on the current Tree Seed Zone Map (1973) and elevation bands within zones.
3. To provide provisional guidelines for seed transfer in artificial regeneration and for breeding zone delineation in the event that current zones are not appropriate.

This paper is a companion to Sorensen and Weber (1994), which describes geographic variation in ponderosa pine in a 290-kilometer band east to west, from the crest of the Cascade Range east across the Deschutes, Ochoco, and Malheur National Forests between latitudes 43°22' N. and 44°34' N. or between townships 12 S. and 25 S. (fig. 1). The present study extends north and south of this band in Oregon and includes only a few samples from the Ochoco and Malheur National Forests.

Collections of wind-pollinated cones were made at 227 locations primarily on the east slopes of the Cascade Range and in the Warner and Ochoco Mountains but also at sites in the Columbia Gorge, canyons in the high desert, and the Lost Forest (Berry 1963) (fig. 1). At 80 locations, cones were collected from two trees separated by 100 meters or more but representing the same site conditions. Pairs were used to obtain a pooled estimate of variance among families-in-locations. The remaining 147 locations were represented by single families. In the main ponderosa pine range, the intensity of sampling was about one location per two townships (per 18 500 hectares). Sample locations were closer together if local elevational or site differences warranted.

The following information was recorded for each location: latitude (in degrees), distance (in kilometers) from the crest of the Cascade Range, elevation (in meters), aspect (in degrees azimuth from north), slope (in degrees), and seed zone (Tree Seed Zone Map 1973).

Location variables were entered into regression equations as latitude (L) in degrees minus 40, distance (D) east (west is negative) of the Cascade crest in kilometers, and elevation (E) in meters. Slope and aspect, both in degrees, were transformed (Stage 1976) to three variables: tangent slope (S), sine aspect \times tangent slope (T1), and cosine aspect \times tangent slope (T2).

Materials and Methods

Sampling

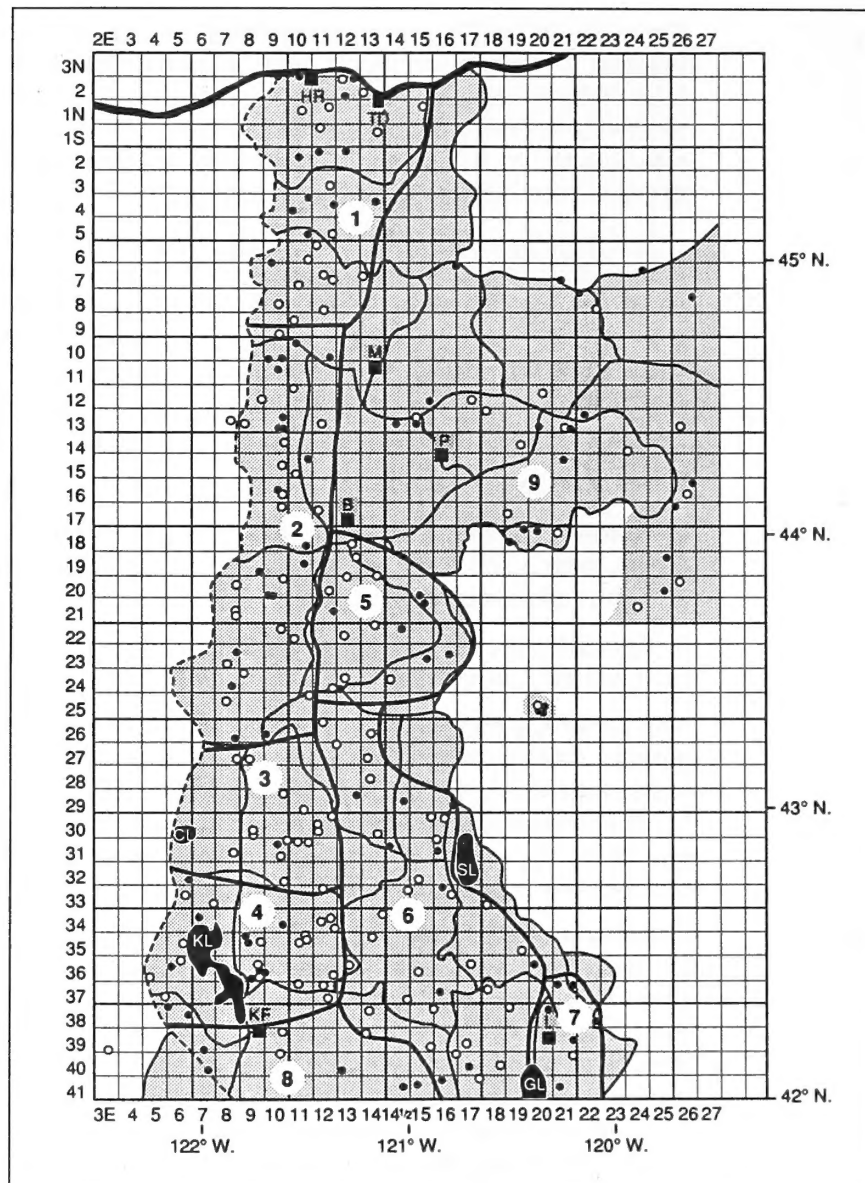


Figure 1—Map of study area in Oregon Cascade Range and central Oregon. Small squares are townships, about 10 kilometers square. Circles are sample locations to nearest quarter of a township. Solid circles represent two families per location; hollow circles represent one. Township numbers (3 N. through 41 S.) are on the left margin; range numbers (3 E. to 27 E.) are given on the horizontal lines. Areas outlined with fine lines are current seed zones (Tree Seed Zone Map 1973). Larger areas with heavier outlines are proposed new zones. Other geographic landmarks are the Cascade crest (dashed line), the towns of Hood River (HR), The Dalles (TD), Madras (M), Prineville (P), Bend (B), Klamath Falls (KF), and Lakeview (L) and Crater Lake (CL), Silver Lake (SL), Klamath Lake (KL), and Goose Lake (GL).

For some analyses, sample sites were classified by (a) 300-meter elevation bands except for the lowest (301 meters, 49 meters to 350 meters) and highest (313 meters, 1851 to 2164 meters) bands and by (b) variable band widths within seed zones. Variable band widths were used, because both this test and Sorensen and Weber (1994) indicated that elevational clines in some locations become steeper with increasing elevation. For (b), band widths ranged from 400 to 200 meters, were widest at lowest elevation, averaged 300 meters in width overall, and had the same number of bands (7) as (a).

Locations also were classified with a conifer class designation that could be readily identified in the field. The five classes were:

1. Ponderosa pine with western juniper (*Juniperus occidentalis* Hook.) or Oregon white oak (*Quercus garryana* Dougl. ex Hook.) (67 locations).
2. Ponderosa pine only (35 locations).
3. Ponderosa pine with lodgepole pine (*Pinus contorta* Dougl. ex Loud.) as the only associated species (34 locations).
4. Ponderosa pine plus one or more of white fir (*Abies concolor* (Gord. and Glend.) Lindl. ex Hildebr.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), sugar pine (*Pinus lambertiana* Dougl.), and western larch (*Larix occidentalis* Nutt.) (80 locations).
5. Ponderosa pine with one or more of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), western white pine (*Pinus monticola* Dougl. ex D. Don), whitebark pine (*Pinus albicaulis* Engelm.), noble fir (*Abies procera* Rehd.), Shasta red fir (*Abies magnifica* var. *shastensis* Lemm.), and Pacific silver fir (*Abies amabilis* Dougl. ex Forbes) (12 locations). Lodgepole pine and species in group 4 may be present.

Class 1 represented the more xeric locations; class 5 usually indicated a high-elevation location for ponderosa pine. Conifer classes were added only to the analyses of the proposed new zone designations.

Seed Traits

Seed weight (milligrams) was based on two individually weighed seeds with fully developed embryos and megagametophytes, as determined from x rays. **Mean germination rates** (1/day) and **standard deviations of rates** (1/day) were based on two 50-seed samples from each family. Chilling and incubation treatments followed Weber and Sorensen (1990). Seeds were soaked 24 hours in aerated distilled water at room temperature (ca. 22 °C), dipped in Captan solution (1 teaspoon/liter) for 30 seconds, shaken to remove excess solution, and stratified at 2-3 °C for 29 days.¹ Seeds were incubated on moist filter paper in covered petri dishes 9 centimeters in diameter. Incubation was at constant 17.2 °C with 12-hour photoperiod. Two replications were placed in separate commercial incubators, and germination counted for 42 days. Petri dishes were randomly located on shelves in each incubator and systematically rotated daily or at each count to minimize the effect of position in the incubator. Mean rate and standard deviation of the rates for seeds within a petri dish were determined following Campbell and Sorensen (1979).

¹The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

Seedling Traits

Seedlings were raised in four separate tests, each representing a different "environment." Environments consisted of two years of sowing (1986 and 1987) and two air temperature treatments. Air temperatures were "warm," with beds covered with a plastic tent from mid-autumn to mid-spring, and "normal," with beds uncovered. All families were in all four tests. There were two replications in each environment. The intent of multiple environments was to increase the expression of genetic variance (Campbell and Sorensen 1978). Prior to sowing, seeds were pretreated as for the germination test except that stratification period was 60 days. Long stratification was used to promote rapid, uniform emergence in the nursery beds (Weber and Sorensen 1990). Stratified seeds were sown at a spacing of 9 centimeters (between rows) by 7.5 centimeters (within row) in four-tree family row plots, with four plots across the bed. The tests were surrounded by two border rows.

Traits used in the principal component analyses are listed in table 1. Each trait in each of the four environments was analyzed separately following the format in table 2, with each trait in each environment considered as a separate trait. Because of heterogeneity of within-plot variances for top and root dry weights in previous tests (Sorensen 1992), these measures were transformed to logarithms before analysis. All means were based on four plants per plot.

Principal Component Analysis

Components of variance were estimated from each analysis (table 2) for location (σ^2_L), family in location ($\sigma^2_{F/L}$) and error (σ^2). Including the four environments and seed characters, over 100 traits were analyzed. To make the number of traits manageable and include only those with greatest family and location variance, traits for which

$$(\sigma^2 + \sigma^2_{F/L})/(\sigma^2 + \sigma^2_{F/L} + \sigma^2_L) < 0.50 \quad \text{or} \quad \sigma^2_L/(\sigma^2 + \sigma^2_{F/L}) < 0.65$$

were deleted. If two traits satisfied the above conditions but were highly correlated ($r > 0.90$), the trait with the lower value of $\sigma^2_L/(\sigma^2 + \sigma^2_{F/L})$ was deleted. This reduced the number of traits to 10 (table 1). For these 10 traits, components of variance and covariance were calculated for each trait and trait pair (Griffing 1956, Kempthorne 1957). Genetic correlations were calculated at the location and family-in-location levels (Campbell and others 1989, Morrison 1967). Principal component analysis was run with the matrix of location-level correlation coefficients as input (SAS Institute 1987). Factor scores were calculated for each family ($n = 307$) from the eigenvectors of the first four principal components. Geographic patterns of genetic variation among families were evaluated by regressing factor scores of the first three principal components against site variables or by hierarchical analysis using site classification models. The fourth principal component was not included in the geographic models, because its plots against geographic variables were relatively flat for all location variables; that is, the difference between locations did not exceed acceptable risk except at extreme distances.

Regression Analysis

Geographic predictor variables were latitude, distance from the Cascade crest, elevation, and the three slope-aspect transformations described above. Factor scores were fitted to a model based on the six location variables. It initially included 86 linear, quadratic, linear \times linear, quadratic \times linear, linear \times linear \times linear terms, and cubic, quartic, and quintic terms for latitude alone and latitude in interaction with distance. Two procedures were used to build the regression models and are described in Sorensen and Weber (1994). The best model was assumed to be the one that explained the greatest amount of location variation with fewest terms and least lack of fit.

Table 1—Description of traits included in the principal component analysis

Trait	Description	Units	Environment ^a
Measured seedling traits:			
1. Time to emergence	Based on 20 seeds per plot	Days to 50% emergence	86-W
2. Date of budset, year 1	First bud scales, observed weekly	Date of 50% budset	86-W
3. Secondary needle score	Scaled, 0 = no secondary needles, 1 = 1-5 fascicles, 2 > 5 fascicles	Score	87-W
4. Needle length	Length of mature 2d-year needle fascicle	Millimeters	86-W
5. Height—3F	Total height at end of year 3	Centimeters	86-W
Derived seedling traits:			
6. Early height growth ratio—2	Early elongation yr 2 ÷ total elongation yr 2	Value < 1	87-W
7. Late height growth ratio—2	Late elongation yr 2 ÷ total elongation yr 2	Value < 1	87-N
8. Early height growth ratio—3	Early elongation yr 3 ÷ total elongation yr 3	Value < 1	87-N
9. Relative elongation rate—3	(Log _e height 3 minus log _e height 1) ÷ 2	Centimeter*centimeter ⁻¹ *year ⁻¹	86-W
10. Form-1	Height:diameter ratio yr 2	Ratio	86-N

^aEnvironments in which the traits were measured are designated by 86 or 87 (1986 or 1987 sowing) and N or W (normal or warm environment); for example, 86-W.

Table 2—Analysis of variance format for individual traits in each environment

Sources of variation	Degrees of freedom	Expected mean squares
Total	613	
Replications	1	
Locations	226	$\sigma^2 + 2 \sigma^2_{F/L} + 2.7034 \sigma^2_L$
Families in locations	80	$\sigma^2 + 2 \sigma^2_{F/L}$
Remainder	306	σ^2

Lack of fit to the selected equations was tested by using as repeats family values from the 80 locations represented by two families each (Draper and Smith 1966). It was assumed that all populations had similar levels of within-location genetic variation, $\sigma^2_{F/L}$ (Hamrick 1976). Additive genetic variance among half-sib (open-pollination) families within locations, σ^2_A , was estimated as $3\sigma^2_{F/L}$. The coefficient, 3, assumed a genetic correlation of 0.33 among offspring of wind-pollinated parents. The value adjusted for some mating among related trees within stands (Squillace 1974) and a low level of natural selfing (Sorensen, in press). Bias also was evaluated by using Mallows' Cp statistic with s estimated by variance among families in locations (Daniel and Wood 1971).

Lack of fit to the geographic models is caused by location variation not explained by the selected regression equation. A good model for guiding seed transfer should include little lack of fit to the selected terms (Campbell 1991). Lack of fit, when significant, could involve several factors: sampling error associated with one or two families per location, possible lack of local adaptation, or geographic terms such as soils, slope position, and so forth, not determined for the locations.

Classification Analysis

Locations were initially classified by seed zone (fig. 1, units outlined by light lines) and 300-meter elevation bands within zones. Variance components were estimated from a random nested model:

$$Y_{ijkl} = \mu + Z_i + E_{ij} + L_{ijk} + F_{ijkl},$$

where μ = grand mean, Z = effect of seed zone (Tree Seed Zone Map 1973), E = effect of elevation band in seed zone, L = effect of location in elevation band, F = effect of family in location, and Y_{ijkl} = the value of the l^{th} family in the k^{th} location in the j^{th} elevation band within the i^{th} zone. All subsample levels had unequal numbers.

Components of variance for seed zones (σ^2_Z), elevation bands in zones ($\sigma^2_{E/Z}$), and locations in elevation bands in zones ($\sigma^2_{L/E/Z}$) were estimated for each of the factor scores. According to the seed zone model, σ^2_Z and $\sigma^2_{E/Z}$ should explain the variation among locations. Lack of fit to the classification model, therefore, was represented by $\sigma^2_{L/E/Z}$. As with the regression model, lack of fit to model was tested against variance among families in locations.

Using visual inspection of plots of regression equations based on the first three principal components (see below) and contour plots of factor score-1, attempts were made to realign seed zone boundaries and combine zones into proposed new zones. Lack of fit was used to compare the ability of the various classification models to explain geographic variation.

Because lack of fit was significant, two other classifications were tried as described earlier. First, the original zone model was used with different widths of elevation bands, and second, a conifer classification (ponderosa pine only and in four mixtures) was added to the 300-meter model for proposed new zones. Conifer classes were within elevation bands, modifying the previous model to,

$$Y_{ijklm} = \mu + Z_i + E_{ij} + C_{ijk} + L_{ijkl} + F_{ijklm},$$

where C_{ijk} = the j^{th} stand designation or conifer class within elevation band within zone, and with $k = 1, 2, \dots, 5$.

Seed-Transfer Risk Evaluation

Risk associated with transfer of seed between locations (TR) is defined as the adaptive genetic mismatch between the population of seedlings being transferred and a population of seedlings native to the planting site (Campbell 1986). Lack of overlap of the distribution curves of the two populations is assumed to indicate the proportion of plants potentially at risk over a rotation. For purposes of estimation, I assumed that the local population represented adaptation to the site ($TR = 0$), and deviations from the local population would result in risk that some plants of the transferred population are nonadapted. Additive genetic variance among pooled families-in-locations, calculated as $3\sigma^2_{F/L}$, was again used to estimate within-location genetic variance.

Average seed transfer risk among locations in elevation bands in zones (TR_w) was estimated assuming that $\sigma^2_{L/E/Z}$ was normally distributed. Mean distance between any two points under the curve (X_d) was estimated as $2\sigma^2_{L/E/Z} (1/\pi)^{1/2}$ (Patel and Read 1982). Transfer risk (TR_w) associated with this mean distance is an estimate of combined risk. It represents the proportions (P) of the normal curves that do not overlap for the traits included under principal components-1, -2, and -3. It was calculated as,

$$TR_w = P_1 + P_2 + P_3 - (P_1 \times P_2 + P_1 \times P_3 + P_2 \times P_3) + P_1 \times P_2 \times P_3.$$

Because the estimate of $\sigma^2_{L/E/Z}$ included error associated with sample sizes of one and two families per location, and genetic factors such as drift and nonlocal wind pollination, I have assumed that half of TR_w represented sampling errors and half represented adaptive differences associated with random seed transfers within an E/Z. TR_w values given subsequently have been adjusted and represent the true estimated risk associated with a seed or plant transfer.

Campbell (1986) and Westfall (1992) both have proposed methods for calculating risk when risk is estimated from more than one variable (more than one principal component in the present example). I have used the method of Campbell (1986), which is a little more conservative than that of Westfall (1992); that is, the same seed transfer gives a slightly lower estimate of risk with the Westfall equation (Sorensen and Weber 1994). In all calculations of risk, I have chosen to use the procedure that would give the higher value of TR.

In the following presentation, TR and TR_w estimate the proportion of plants in the seedling population that is presumed to be at risk, in the course of a rotation, from some type of environmental damage for adaptive reasons. $TR = 0.4$ implies that 40 percent of the seedling plants are outside the genetic distribution of the native population and potentially at risk over the course of a rotation. Risk values are indicators of relative, not absolute, risk and have not been field tested. Risk does not necessarily imply mortality, but rather lack of ability to respond to site conditions as would the local population. In addition, TR does not include loss or damage from mechanical factors such as browsing and trampling. Planting density would have to compensate for this potential loss in addition to potential adaptive mismatch, TR. For purposes of field guidance, $TR \leq 0.51$ is assumed acceptable. This risk level is based on a planting density of 1,076 seedlings per hectare (3.05- by 3.05-meter spacing), 30 percent loss due to random mechanical factors, and assumes that 16 percent of the planted trees (172 trees per hectare) are targeted as crop trees (further description given in Sorensen and Weber 1994).

Results

Mean sample latitude was 43°35' N., mean distance was 62 kilometers (range, -31 to 188 kilometers), mean elevation was 1397 meters (range, 49 to 2164 meters), and mean slope was 6° (range, 0 to 40°). Three of the linear correlations among geographic variables identifying locations were significant. Elevation of sample locations decreased with latitude ($R = 0.449$, $p < 0.001$) and increased with distance from the Cascade crest ($R = 0.116$, $p < 0.001$), and distance of sample locations from the crest decreased slightly with latitude ($R = 0.047$, $p < 0.001$). Elevation had a strong inverse correlation with latitude, because of very low-elevation locations in the north near the Columbia River (down to 49 meters). The positive relation between distance and elevation was partly due to the same cause—the low-elevation locations near the Columbia River also were relatively close to the Cascades. Also, south of about 43°30' N., a decrease in elevation occurs within 30 to 50 kilometers east of the Cascade crest, but further east the general land mass and ponderosa pine occur at increasingly higher elevations.

The year of sowing had a minor affect on first-year phenology. Mean time to emerge was 21 days after sowing in 1986, 15 days after sowing in 1987; mean date of first year bud set was September 6 in 1986 and September 8 in 1987. At the end of

3 years, seedlings sown in 1987 were 6 percent taller, 2 percent smaller in diameter, and equal in dry weight to seedlings sown in 1986. Covering with a plastic tent in winter increased final height, diameter, top and root dry weights, and needle length by 14 percent, 11 percent, 20 percent, 14 percent and 30 percent, respectively.

Factor Scores

The 10 traits included in the principal component analysis reflected seedling vigor (needle length, final height, relative elongation rate), phenology (dates of emergence and bud set, late and early height growth ratios), form (height:diameter ratio), and a secondary needle score trait. In general, the analysis was less heavily weighted to seedling size traits than has been the case previously in our tests (for example, Campbell and Sugano 1987, Sorensen 1992). The first three components explained 77 percent of the location-related variance in the 10 diverse seedling variables (table 3). The fourth component added 10 percent more.

Factor score eigenvectors indicated that principal component-1 was primarily size related (table 3). Large scores identified locations with tall, slender seedlings and with large rate of elongation overall, but proportionately little elongation early in the season. Principal component-2 was loaded most heavily for phenology and needle traits. Locations with large scores had seedlings that emerged early and set bud early and developed a high frequency of secondary needles the first year and long needles in year 2. Large principal component-3 scores were associated with locations whose seedlings put on proportionately much of their elongation relatively late in the extension period. Principal component-4 was loaded most heavily for emergence time; large scores identified locations whose seedlings emerged late.

Regression Analysis

Linear correlations between factor scores and different location variables are given in table 4; summaries of the multiple regression equations are in table 5. Similar to an earlier test with ponderosa pine from the Ochoco Mountains of central Oregon (Sorensen and Weber 1994), multiple regression equations were complex and included considerable effect of terms involving slope and aspect (table 5, last 3 lines). Factor scores for all four principal components were significantly related to location variables in multiple regression, but only one, factor-1 scores, had an $R^2 > 0.30$ (table 5).

Table 3—Principal components (PC) with loadings, eigenvalues, and percent of location variance explained by principal components

Trait ^a	Loadings			
	PC-1	PC-2	PC-3	PC-4
1. Emerge	-0.058	-0.399	0.224	0.666
2. Budset	.230	-.440	.360	.024
3. Secondary needle score	.195	.482	.094	.031
4. Needle length	.248	.452	.191	.379
5. Final height	.440	.181	-.058	-.029
6. Early height ratio-year 2	-.446	.231	-.192	.071
7. Late height ratio-year 2	-.125	.226	.752	.004
8. Early height ratio-year 3	-.353	.240	-.126	.476
9. Elongation rate	.332	-.089	-.390	.422
10. Height-diameter ratio-year 2	.448	.083	-.037	.013
Eigenvalue	4.660	1.712	1.313	1.026
Variation explained ^b	46.6%	17.1%	13.1%	10.3%

^a Additional information on the traits is in table 1.

^b Percentage of location-related variation in the measured traits explained by the principal components.

Table 4—Linear correlation coefficients between factor scores (FS) for 4 principal components and geographic and topographic variables for the locations where seeds were collected

Location variable	FS-1	FS-2	FS-3	FS-4
Latitude	0.144* ^a	-0.054	-0.037	0.112
Distance	-.205**	.026	-.187**	-.298***
Elevation	-.542***	.039	-.178**	-.041
Aspect:				
East-west deviation ^b	-.064	.013	.020	-.091
North-south deviation	.075	.029	.014	-.001
Slope	-.005	-.049	-.071	-.043

^a Significance levels are *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

^b "Deviation" is based on a transformation given by Stage (1976).

Lack of fit to the multiple regression models was highly significant for all principal components. This suggests that geographic factors other than those included in the regression model are influencing factor scores. However, because lack of fit would include sampling errors and because F-values for lack of fit were small (table 5), it is assumed that lack of fit can be ignored in interpreting the regression results.

Principal component-1— R^2 for locations was 0.69 (table 5). Scores increased with latitude, decreased with distance from the Cascade crest, and decreased greatly with elevation (table 4), with rate of decrease increasing with elevation. Slope and aspect variables were important for this component. Figure 2 shows the relation of factor scores to latitude and elevation at one distance from the Cascades in southern Oregon.

Principal component-2—Regression explained 29 percent of the variance among locations, but most of the variation was associated with slope and aspect variables and their interaction with location (table 5).

Principal component-3—Scores increased with elevation and distance from the Cascades (fig. 3). Most of the location variance explained by regression was associated with geographic terms.

Principal component-4—Scores decreased slightly with distance from the Cascades and were not affected by topographic variables (fig. 4 and table 5).

In general, measures of seedling vigor and size decreased with elevation and, to a lesser extent, with distance from the Cascade crest and increased with latitude. Because elevation increased with distance and decreased with latitude, it seems likely that elevation is the overriding factor associated with variation in vigor. Figures 5 and 6 are diagrams in which five levels of factor score-1 are plotted by latitude and longitude (not distance in this case) (fig. 5) and by latitude and elevation (fig. 6). Symbols in figures 5 and 6 indicate five divisions of factor score-1, each division including two factor score units.

Although elevation dominates the differentiation pattern, there appear to be three marked deviations from the main elevational pattern. Between 42° and about 42°30' N., there are several "+" values where "0" is expected based on the general trend (fig. 6); that is, locations in this area have given more vigorous progenies in the common garden than expected based on their source elevation. Farther north between about 43° N. and 44° N. and near the Cascades is an area where factor scores for principal component-1 seem lower (the plants less vigorous) than the elevation warrants (fig. 6). The location of this area is shown on figure 5 by the elongated group of "-" symbols between 43.25° N. and 44° N. and farthest to the west. Finally, at about 44°30' N., two "+" marks and two "0" marks occur at higher elevation than the general trend indicates that they should (fig. 6).

With regard to other potentially adaptive traits, stockiness also increased with increasing elevation and distance from the Cascades. The effect of elevation often tended to be greater at high than at low elevation and farther away from than closer to the Cascades. For phenology in the common garden, first-year bud set occurred earlier and second- and third-year extension growth started earlier and ceased earlier with increasing elevation and increasing distance from the Cascade crest

Text continues on page 15.

Table 5—Descriptive characteristics of multiple regression equations relating seed source factor scores to geographic and topographic location variables

Characteristic	PC-1	PC-2	PC-3	PC-4
Number of significant ($p = 0.05$) terms in equation	35	34	12	13
R^2 for locations (percent of location variance explained by regression)	69.1	29.1	20.0	24.5
Lack of fit tests:				
F-values	1.85	2.06	1.71	1.79
Degrees of freedom	191,80 ^a	192,80	214,80	213,80
Probability, $p =$	0.0010	0.0002	0.0031	0.0016
Sums of squares (type II, ^b in percent) explained by:				
Geographic terms	24	6	41	30
Geographic \times geographic terms	21	4	45	70
Topographic terms	4	8	0	0
Topographic \times topographic terms	4	12	0	0
Geographic \times topographic terms	47	70	14	0

^a 1st number = lack of fit (error from regression analysis less families in locations), and 2d number = pure error (families in locations).

^b SAS Institute 1987: 96-98. Values are the percentages of total type II regression sums of squares that were due to simple geographic terms (latitude, distance, and elevation), 1st line; to geographic \times geographic interaction terms, 2d line; to simple topographic terms (the 3 slope-aspect transformations), 3d line; and so forth.

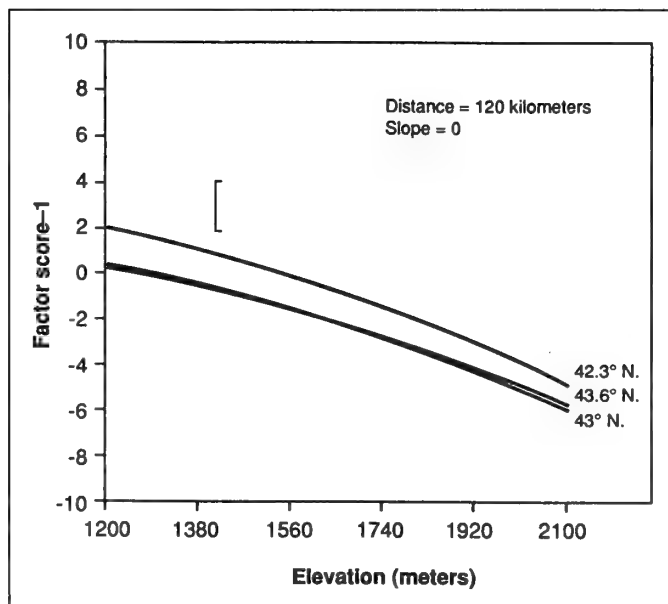


Figure 2—Relation between factor scores for principal component-1 and elevation at three latitudes in southern Oregon, other factors constant at slope = 0 percent and distance = 120 kilometers east of the Cascade crest. Plotted lines span the elevational distribution of ponderosa pine at these latitudes and distance. The vertical line is equal to one standard deviation of within-location additive genetic variance of factor score-1 and is equivalent to a transfer risk of 0.38.

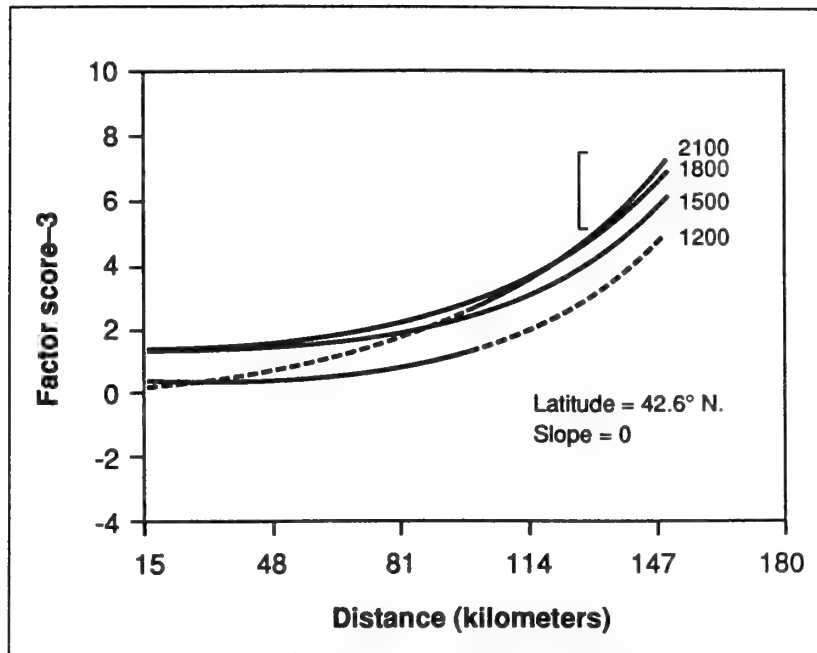


Figure 3—Relation between factor scores for principal component-3 and distance from the Cascade crest at four elevations, other factors constant at slope = 0 percent and latitude = 42.6° N. Dashes indicate no ponderosa pine at these locations. The vertical line is equal to one standard deviation of within-location additive genetic variance of factor score-3 and is equivalent to a transfer risk of 0.38.

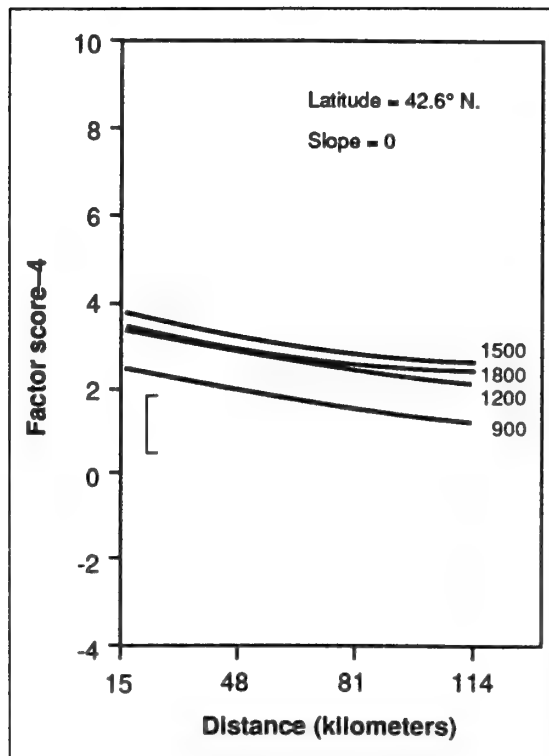


Figure 4—Relation between factor scores for principal component-4 and distance from the Cascade crest at four elevations, other factors constant at slope = 0 percent and latitude = 43° N. The vertical line is equal to one standard deviation of within-location additive genetic variance of factor score-4, and is equivalent to a transfer risk of 0.38.

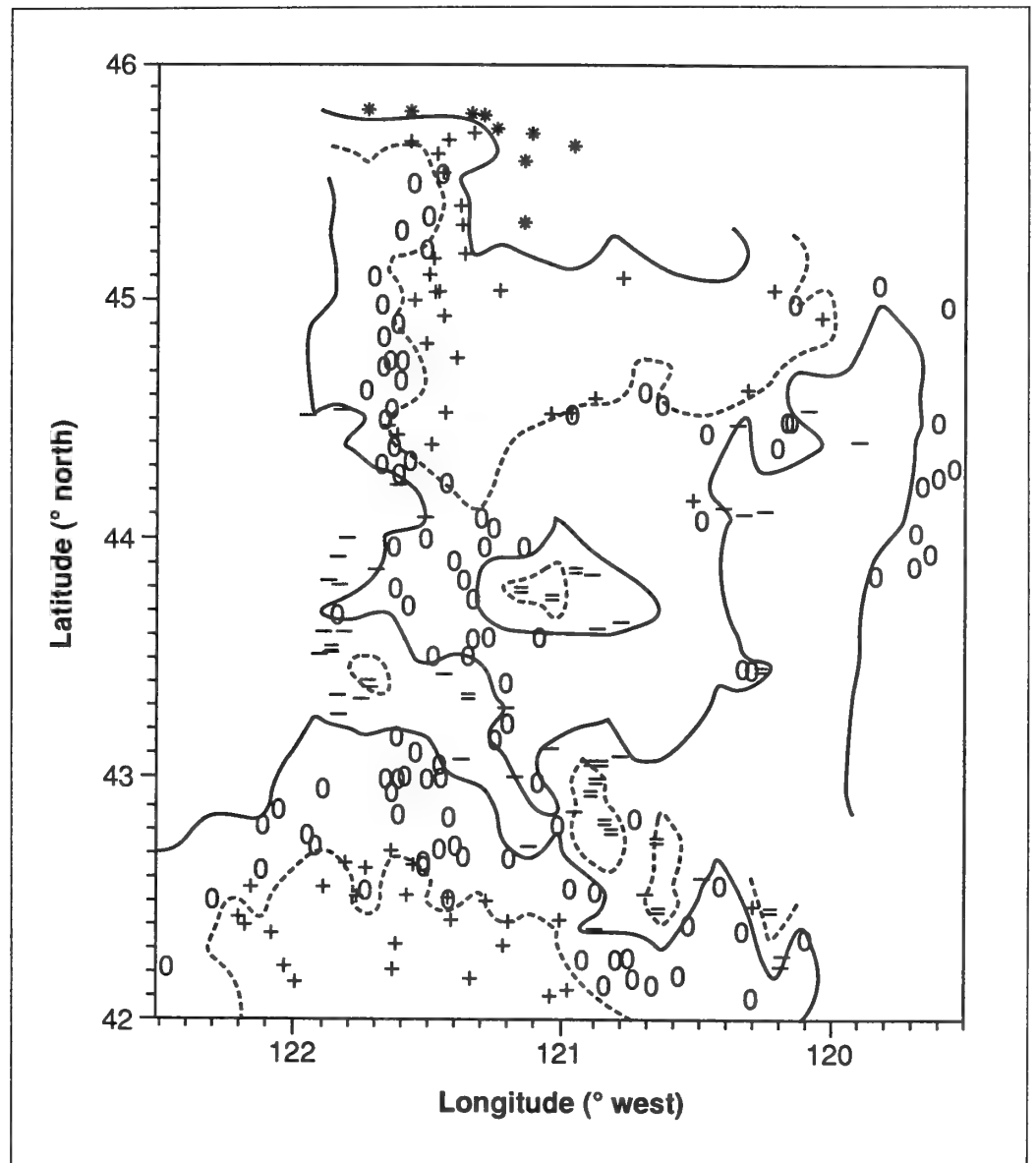


Figure 5—Factor scores, in five classes, for principal component-1 plotted by latitude and longitude. Factor scores are not adjusted for elevation. Principal component-1 is associated primarily with vigor traits. Symbols grade from = (lowest factor-1 scores, least vigor) through -, 0, +, to * (highest factor-1 scores). Lines, with a few exceptions due to local wide elevation variation, enclose common symbols.

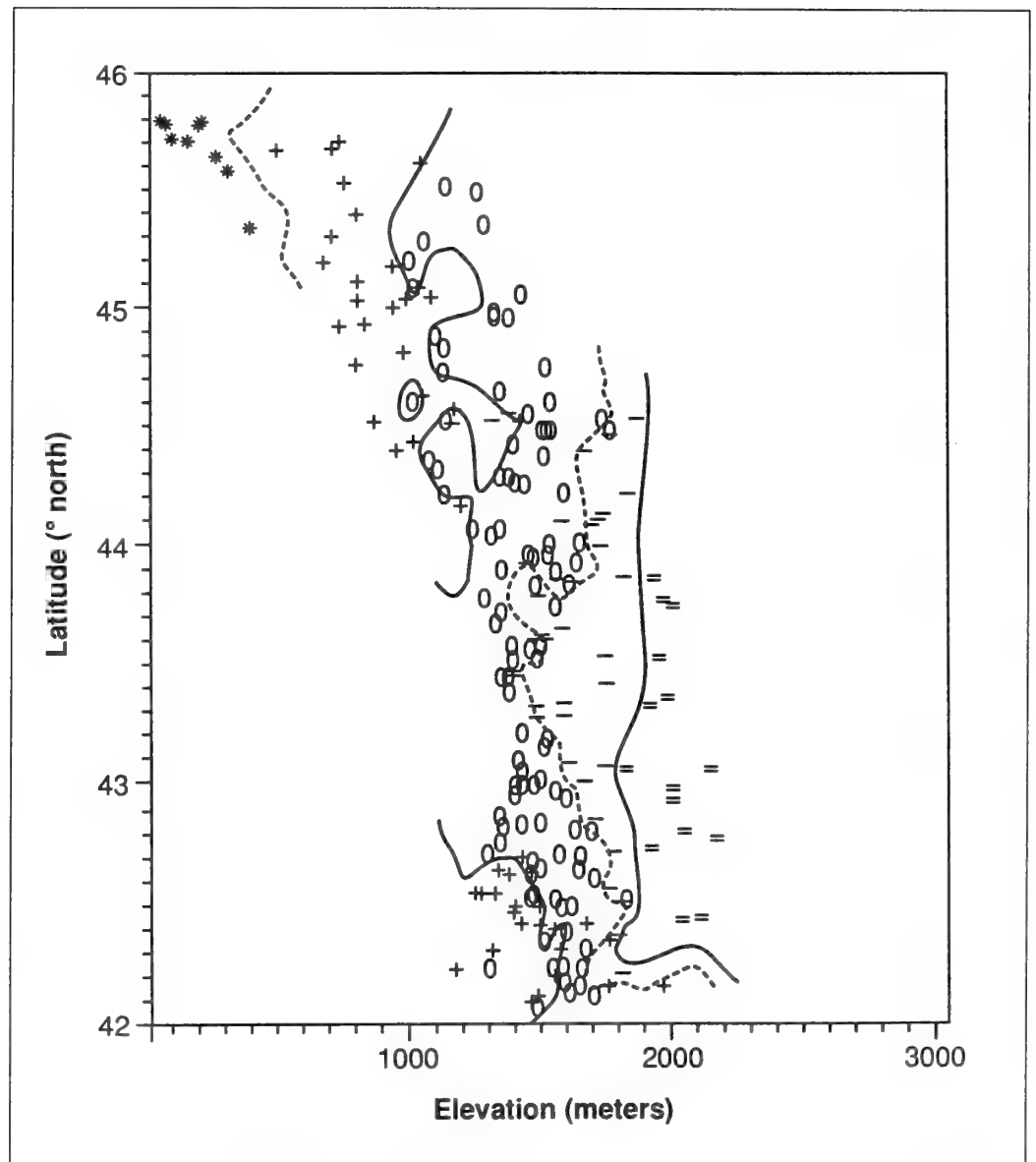


Figure 6—Factor scores, in five classes, for principal component-1 plotted by latitude and elevation. Scores are not adjusted for latitude. Principal component-1 is associated primarily with vigor traits. Symbols grade from = (lowest factor-1 scores, least vigor) through, -, 0, +, to * (highest factor-1 scores). Lines, with a few exceptions, enclose common symbols.

Table 6—Components of variance^a for factor scores of the 1st 4 principal components (PCs) in percentage of total location variance for seed zones (σ^2_Z), 300-meter elevation band in zones ($\sigma^2_{E/Z}$), locations in elevation bands in zones ($\sigma^2_{L/E/Z}$), and ratio of total components of variance for location to component of variance for families-in-location ($\sigma^2_L : \sigma^2_{F/L}$)^b

Trait	σ^2_Z	$\sigma^2_{E/Z}$	$\sigma^2_{L/E/Z}$	$\sigma^2_L : \sigma^2_{F/L}$
Current zones:				
Factor score-1	22* ^c	57***	21***	2.92
Factor score-2	3	-17	114***	1.09
Factor score-3	11	5	84***	.77
Factor score-4	22*	13	65***	.92
Proposed zones:				
Factor score-1	8	58***	34***	2.46
Factor score-2	2	-7	105***	.78
Factor score-3	27***	-5	78***	1.00
Factor score-4	8	23**	69***	.91

^a Components calculated from Type I sums of squares (SAS Institute 1987, pages 95-96).

^b Results are given for the current designation (Tree Seed Zone Map 1973) with 31 zones and for a proposed group of 9 zones.

^c Levels of significance are *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Classification Analysis

Results of analysis of the classification model using 300-meter elevation bands are given in table 6. Lack of fit ($\sigma^2_{L/E/Z}$) to the model was very highly significant in all cases. Because of the curvilinear relation between factor score and elevation (example, fig. 2), a second classification using the same number of bands but of graduated width, wider at the bottom, narrower at the top, was also tried. This had a negligible effect on $\sigma^2_{L/E/Z}$, reducing it for principal component-2 but increasing it slightly for principal components 1, 3, and 4.

New Zone Designations

Both regression plots (figs. 2 to 4) and the small zone effect (table 6) in the classification analyses indicated that breeding blocks for ponderosa pine could be considerably larger in latitude or longitude than are current seed zones. To define the new zones, a large number of regression plots (figs. 2 to 4 are examples) were made of factor scores for the first three principal components, and contour maps were developed from factor scores of principal component-1 only (figs. 5 and 6). From these, nine new geographic zones were outlined (fig. 1). The adequacy of the new zones was then checked with additional classification analyses and by calculating risk estimates for random transfers within zones and elevation bands. The new classification, on the average, had slightly greater lack of fit than the old; principal component-2 was an exception. Subsequent testing with the risk equation (see below) indicated

that the increased lack of fit could be tolerated. The new classification also was tried without zone 9, which was large and generally outside the area of interest for planting and seed transfer. Lack of fit was decreased slightly for principal component-1 and increased slightly for the other three. Overall, the change was negligible and zone 9 has been left in. Finally, the five conifer classifications were added to the new model and the analyses repeated. The result was a very slight increase in the F-values for lack of fit for all principal components compared to the nine-zone model. In other words, conifer classes reduced sums of squares to almost the same extent that they reduced degrees of freedom. Conifer classes were not associated with adaptive variation within zones.

Verification of the Nine-Zone Classification Model

The model was verified in two ways. Mean distance between two points within the average proposed zone was computed by using the equation of Patel and Read (1982), and the risk, TR_w , associated with a transfer of this distance was calculated for the first three principal components. The calculated mean value was 0.53. Assuming that half of this value was due to random fluctuations (for example, sampling or genetic drift) (Sorensen 1992), the average movement within a new zone and elevation band had an adaptive risk (TR_w) of 0.255; that is, about 25 percent of the seedlings transferred would represent an adaptive mismatch to the planting site. It was interesting that when TR_w was computed for the old zones (Tree Seed Zone Map 1973), the value was larger (0.58, $TR_w = 0.29$) than for the proposed zones. This occurred solely because the old zones, even though there were more of them, had a considerably larger lack of fit for principal component-2 than did the new zones. In other words, even though the new zones are larger, the use of regression plots to delineate them improved the zone definition.

Transfer risk also was calculated for 210 seed transfers within proposed zones and within 300-meter elevation bands. Calculations were made for transfers between actual pairs of sample locations. Again, risk was cumulative risk associated with principal components 1, 2, and 3. Although the pairs were not chosen purely at random, they represented the range of distances that would occur in seed transfer within a zone. The results of this exercise are given in table 7. The weighted mean risk was 0.235, about the same as that determined for TR_w . The maximum $TR = 0.71$; five estimates of TR were > 0.51 . In addition, 78 transfer risks were calculated between neighboring blocks, but in the same elevation band. Mean $TR = 0.293$ with 3 of the 78 estimates of $TR > 0.51$.

Discussion Geographic Variation

The elevational cline seemed to dominate source-related genetic variation. Significant location effects were associated with latitude and distance from the Cascades, but because latitude and distance were correlated with elevation, it was hard to separate their influence from that of elevation. Rehfeldt also found in common garden studies of ponderosa pine in the northern Rocky Mountains that geographic clines for ponderosa pine across latitude and longitude are quite gentle (1984) but are relatively steep for elevation, and he emphasized the close association between elevation and various components of shoot elongation (Rehfeldt 1986a, 1986b). Recommended discrete zone elevational bands for var. *ponderosa* in the Rocky Mountains were 400 meters with transfers from a single source limited to plus or minus 200 meters (Rehfeldt 1986a, 1986b, 1991). Narrower elevation bands (about 250-meter discrete zones) were recommended for var. *scopulorum* (Rehfeldt 1990, 1993).

Table 7—Calculated risk estimates (TR) for seed transfers between pairs of sample locations within the 9 proposed new zones and within 300-m elevation spreads within these zones

Zone	Transfers	Mean R ^a	Maximum R ^a	R > 0.51
	<i>Number</i>			<i>Number</i>
1	25	0.178	0.337	0
2	28	.287	.714	2
3	14	.197	.430	0
4	32	.160	.330	0
5	18	.143	.389	0
6	40	.288	.516	1
7	11	.425	.606	2
8	10	.298	.466	0
9	32	.240	.479	0
Weighted average		.235		

^a R-values are combined estimates based on the 1st 3 principal components

Although elevation seemed to dominate geographic differentiation, there were three notable exceptions to the general elevational pattern. In the extreme south, seedlings from relatively high-elevation locations had large factor-1 scores (vigor principal component) in the common garden. At this latitude, the distribution of ponderosa pine is continuous across the Siskiyou Mountains and Cascade Range. The “+” scores (fig. 6, bottom) at relatively high elevation may reflect a Pacific Coast climatic influence at the inland sites and local adaptation to it. The Klamath River, like the Columbia, cuts through the Cascade Range. It forms a drainage from Klamath Falls just north of 42° N. lat. to the Pacific Ocean, which it enters at about 41° N. A sampling of weather stations (Johnsgard 1963) near the Cascades and farther inland between 42° N. and 43° 30' N. is given in table 8. Although elevation of the stations is not uniform, two weather characteristics that should show maritime influence (frost-free period and daily temperature amplitude) both indicate a milder climate near 42° N. than near 43° N. The Klamath River drainage may allow some moderating maritime environmental influence to penetrate into south-central Oregon.

Table 8—Records from selected weather stations near the Cascade Range in southern Oregon and near the Warner Mountains and Winter Ridge 80 to 110 kilometers farther inland

Station name	Latitude	Longitude	Elevation	Mean annual temperature	Frost-free period	Temperature amplitude ^b
	[°] N	[°] W	Meters	[°] C	Days	[°] C
Stations near the Cascades:						
Klamath Falls	42°13'	121°47'	1260	9.1	164	13.5
Chiloquin	42°35'	121°52'	1280	7.0	73	19.4
Chemult	43°14'	121°47'	1450	5.2	11	18.2
Crescent	43°27'	121°42'	1360	5.1	— ^c	20.2
Stations inland from the Cascades:						
Lakeview	42°12'	120°22'	1460	7.8	122	15.4
Valley Falls	42°29'	120°16'	1310	8.1	98	17.4
Paisley	42°44'	120°33'	1330	9.2	144	15.3
Lake	43°13'	120°38'	1310	7.2	— ^c	19.3
Fremont	43°19'	121°09'	1310	5.9	21	19.8

^a Number of days between last spring and first autumn temperatures of -2.2 °C.

^b Difference between mean annual maximum temperature and mean annual minimum temperature.

^c — = value for frost-free period was not available.

The second anomalous area contains a group of 11 locations between 43°12' N. and 43°50' N. and between 11 and 24 kilometers (mean 16 kilometers) east of the Cascade crest. They are the most westerly sample locations in this area (figs. 1 and 5). Elevation of the 11 locations ranged from 1329 to 1582 meters (mean 1470 meters). Principal component-1 factor scores for the 11 locations ranged from -0.94 to -1.85 (mean -1.32) with 10 of the scores < -1.20. There were 85 other locations in the test between 1329 and 1582 meters. Only 8 of the 85 locations had factor scores for principal component-1 < -0.94, and 4 of those were in the Ochoco Mountains. In other words, the area between 43°12' N. and 43°50' N. and 10 to 25 kilometers from the Cascade crest supported ponderosa pine whose seedlings were of lower vigor than expected, based on other seedlings of comparable elevational origin in the common garden. This area shows up on some of Alsop's (1980) topothermal maps for western Oregon as having low temperature minima and relatively strong continentality. The affected area is just north of Crater Lake and surrounding peaks. Immediately to its west, the Cascade crest is quite high, averaging about 1950 meters between 43°10' N. and 43°50' N. Elevation falls off quickly east of the crest to a rolling, but relatively

uniform, topography. Low-elevation flats in the rolling area are occupied by lodgepole pine as a topographic climax, because of temperatures too cold for ponderosa pine to successfully regenerate (Cochran and Berntsen 1973). Thermal properties associated with the pumice-mantled high plateau (Cochran 1975, Cochran and others 1967) plus cold air drainage from the high ridge of the Cascades may result in temperatures throughout the indicated area that are relatively low for the elevation. Factor-1 scores in general showed considerable sensitivity to elevation and presumably to temperature. Low scores at low elevation would represent adaptation to a climate created by the local radiational situation and accentuated by cold air drainage.

Third, are the four locations near 44°30' N. that plot as having high factor-1 scores for their elevation (fig. 6). Three of these locations were from semi-isolated stands in the high desert between the Cascade Range and the Ochoco Mountains, two at mid and high elevation on Grizzly Mountain and one on Pine Ridge in the Crooked River National Grassland. Again, I can only speculate that temperature is the controlling factor. I assume that at comparable elevations, temperatures are often more moderate on isolated peaks and ridges than they are on more extensive land masses. Even though growth at the sites themselves is poor, ponderosa pine seedlings from them evidently have considerable potential for growth and respond comparatively vigorously in a common garden where conditions for growth are favorable.

The largest within-zone and elevation band TR-values were in zone 7 (table 7), a small zone encompassing the Warner Mountains in Oregon. Two explanations are possible. The zone is on the distance and latitudinal edge of the sample area, and it had the highest mean elevation and greatest mean slope. This edge position may have resulted in poorer fit to the regression model. Another possibility is that one or more Washoe pine (*Pinus washoensis* Mason and Stockwell) families were included in the Warner group. Critchfield (1984) locates Washoe pine in the Warners south of the California border. Even though it apparently hasn't been reported in the Oregon Warner Mountains, it may be there. Compared to ponderosa, Washoe pine has low seedling growth potential² (Wells 1964), and if misidentified could have contributed to the large variation within the zone.

Temperature vs. Moisture as Selective Forces for Ponderosa Pine

Test seedlings were cultured in nursery beds in western Oregon where humidity is high, winter precipitation occurs as rainfall, and soil becomes saturated over winter and remains wet well into the next growing season. Beds to be covered with plastic tent (warm environment) were not covered until the beds were well watered with autumn rains. It was under these conditions that source-related variation in size traits was associated mainly with elevation. Seedlings from low-elevation, extremely xeric sites along the Columbia River had the highest factor-1 (vigor) scores in the common gardens (fig. 6); seedlings of more mesic origin within 40 kilometers, but 1000 to 1200 meters higher in elevation, had lower scores (fig. 6). Field measurement of productivity between the locations these seedlings came from would not be expected to give differences in the same direction (Hamrick and others 1989). Thus, site quality related to moisture, or the xeric-mesic contrast in site physical characteristics, was not a good measure of the potential for growth in ponderosa pine.

²Personal communication. 1993. Gerald Rehfeldt, plant geneticist, Intermountain Research Station, 1221 South Main, Moscow, ID 83843

Rehfeldt has conducted a number of tests with ponderosa pine in which moisture stress was applied in one of the test environments (1986a, 1986b, 1990, 1993). Seedlings responded in a plastic manner to moisture stress with decreased height and reduced needle length, but in no case was there evidence for a genetic response "that could be interpreted as adaptive to different moisture regimes; even under conditions of moisture stress, genetic differences were best interpreted as adaptation to frost-free periods of variable length" (see footnote 2).

A similar observation is reported from another Rocky Mountain test. Madsen and Blake (1977) show that seedlings from a warm, dry habitat at high elevation on a south slope in Idaho grew more vigorously than expected based on elevation of origin in a common garden study that included many families and seed sources.

With regard to genetic differentiation, I hypothesize that elongation potential of ponderosa pine is strongly selected by temperature but is less selected by moisture characteristics of the seed source. That is, the growth potential is plastic if moisture is the selective agent but is more inherently fixed if temperature is the agent, where "plastic" vs. "fixed" are used in the following sense. Seedlings from ponderosa sites that are poor because of a short growing season induced by moisture deficit will respond to favorable growing conditions with increased growth (plastic); seedlings from sites with a short growing season because of low temperature constraints will have much less ability to respond to the same favorable growing conditions (fixed).

Lack of Fit to the Models

Lack of fit is highly significant, but F-values testing it are not large. Because lack of fit also includes some sampling error, it may be questionable that it exists in the sense that there are geographic, topographic, or edaphic factors affecting variation that are not satisfied by the model.

Over most of the sample area, ponderosa pine occurred in large continuous populations. The most broken distribution was in proposed zone 9 (fig. 1), which included four extensive but separated areas (Ochoco Mountains, Maury Mountains, and Snow Mountain District of the Ochoco National Forest, and the western edge of the Umatilla National Forest), one smaller area (Lost Forest), and three small isolated stands in draws in the high desert. In addition, samples from both proposed zones 1 and 8 included isolated stands. Compared to continuous populations, these are conditions that might lead to random genetic differentiation. To the extent that lack of fit includes random causes, lack of fit and transfer risk should be higher for these zones than for the others. Risks for more or less random transfers within zones are summarized in table 7. The weighted mean for zones 1, 8, and 9 is 0.226, which is less than the weighted mean for all zones. This is a coarse comparison, but it does not provide evidence that random genetic events are contributing to differences among localities in seedling morphometric traits in regions where the distribution is discontinuous. This conclusion seems to be in good agreement with isozyme observations of the population genetic structure of Douglas-fir on "island" mountain ranges in the Great Basin of Arizona, Nevada, and Utah (Schnabel and others 1993).

Seed Transfer and Proposed Zones

The transfer risk equation (program available from author) based on the regression model should be the best guide to seed source selection (Rehfeldt 1990). Its use assumes that seeds from various locations are in inventory or can be collected. Transfer risks are calculated between the planting site and potential seed sources. Seed source selection is based on low risk (low TR-value). Among low TR-value sources, a second selection could be based on highest factor-1 scores, factor-1 being associated with seedling vigor. An example of application is given in Sorensen (1992: table 9). The equation is applicable only to native ponderosa pine sites within the sample area. It can not be used to test the risk of transfer to locations within the sample area where ponderosa is not native, or to locations beyond the geographic limits of the sampled region.

For administrative and management reasons, seed collections may be combined (bulked) rather than inventoried separately. The customary alternative to the regression approach is to bulk the seeds within zones and elevation bands. Bulk lots, and there can be several lots per zone, can be used throughout the appropriate zone. For the proposed zones of this test, the estimate of TR_w and the TR-values in table 7 are about 0.25; that is, about 25 percent of the seedlings in the random within-zone transfer would be outside the distribution of values for seedlings native to the planting site. I stress again that TR is a relative, not an absolute, value. In other words, this proportion of plants is considered **potentially** at risk over the course of a rotation for adaptive reasons. TR-values do not include loss to mechanical factors, such as browsing and trampling. Calculation of appropriate planting density would have to consider this type of loss as well as potential adaptive mismatch.

Nine proposed zones are outlined in figure 1 for the area east of the Cascade Range in Oregon. It needs to be emphasized that the lines between zones do not represent breaks in the expression of any traits. Their placement, although based on evaluation of figures 2-6 and other similar diagrams, was simply a convenience for subdividing the area. If management goals would benefit from different placement of the lines, new ones could be drawn and evaluated by computing the risk associated with a number of within-zone seed transfers. For computational purposes, pairs of locations could be furnished from the current study, or other pairs of ponderosa sites within proposed zones could be used to calculate transfer risks.

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Metric and English Units of Measure

When you know:	Multiply by:	To find:
Celsius (°C)	1.8 and add 32	Fahrenheit
Kilometers (km)	0.621	Miles
Meters	3.281	Feet

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Adaptive genetic variation in seed and seedling traits for ponderosa pine from the east slopes of the Cascade Range in Oregon was analyzed by using 307 families from 227 locations. Factor scores from three principal components based on seed and seedling traits were related by multiple regression to latitude, distance from the Cascade crest, elevation, slope, and aspect of the seed source and by classification analysis to seed zone and 300-meter elevation band within zone. A provisional transfer risk equation and tentative new seed zones were delineated to guide seed transfer in artificial regeneration.

Keywords: *Pinus ponderosa*, seedlings, provenance, geographic genetic variation, ecological genetics, genecology, genetic diversity.

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